ANNUAL SURVIVAL AND SITE FIDELITY OF STELLER'S EIDERS MOLTING ALONG THE ALASKA PENINSULA

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Abstract: Populations of Steller's eiders (*Polysticta stelleri*) molting and wintering along the Alaska Peninsula have declined since the 1960's. We captured and marked a large sample of Steller's eiders molting in 2 lagoons along the Alaska Peninsula between 1975–97. We used mark–recapture analysis techniques to estimate annual survival and movement probabilities within and among lagoons for male and female eiders. Estimates of annual survival ($\pm$SE) were 0.899 ± 0.032 for females and 0.765 ± 0.044 for males. Both sexes showed high rates of fidelity to specific molting locations (>95%) within lagoons; yet we found no evidence that annual probability of survival differed among groups molting in different locations either within or among lagoons. We found weak evidence that annual survival decreased between the periods 1975–81 and 1991–97. The lower survival of males compared to females is unusual for waterfowl and may result in a female-biased sex ratio. We conclude that a decrease in adult survival may have initiated the long-term population decline. Further, a shortage of males may be limiting reproductive potential.

Key words: Alaska, band loss, molt, movement probability, *Polysticta stelleri*, site fidelity, Steller's eiders, survival.

Little is known about the life history and biology of Steller's eiders. Steller's eiders breed in Arctic Russia and Alaska (Kertell 1991), however, breeding propensity and success vary annually at specific sites. Male Steller's eiders and non- or failed-breeding females from arctic Russia and Alaska concentrate in several lagoons along the Alaska Peninsula in August and September where they undergo a complete molt of their flight feathers (Jones 1965; Petersen 1980, 1981). Populations of Steller's eiders molting and wintering along the Alaska Peninsula have declined since the 1960's (Kertell 1991). A large portion of the breeding population is thought to winter in these areas (Jones 1965). Concurrent with the decline in the winter population, populations of Steller's eiders breeding on the Yukon–Kuskokwim Delta and Arctic Coastal Plain in Alaska, and in Siberia have also declined (Kertell 1991, Flint and Herzog 1999). Accordingly, the Alaska breeding population of Steller's Eiders was listed as threatened under the provisions of the U.S. Endangered Species Act in 1997 (Federal Register 1997) and received similar designation a decade earlier in the Yakutsk Republic, Russia (Kertell 1991). Thus, it seems apparent that the worldwide population of Steller's eiders is declining, while the cause of this decline is unknown.

In a simplistic model, populations decline when average annual mortality exceeds average annual recruitment. Little is known about either survival or recruitment for Steller's eiders (Bellrose 1980, Kertell 1991). For other species of waterfowl, recruitment varies both regionally and annually, and thus, an overall estimate of recruitment for the population is difficult to determine. Detailed models describing the dynamics of waterfowl populations demonstrate that small changes in adult female survival will have a relatively large influence on population dynamics compared to similar changes in reproductive parameters (Schmutz et al. 1997, Flint et al. 1998). Thus, for declining Steller's Eider populations, we hypothesize that a reduction in adult female survival has initiated the decline.

Many species of waterfowl exhibit high rates of fidelity to breeding areas (Anderson et al. 1992); however, comparable fidelity to molting areas has rarely been studied in detail (Anderson et al. 1992, Hohman et al. 1992). Bollinger and Derksen (1996) reported that black brant

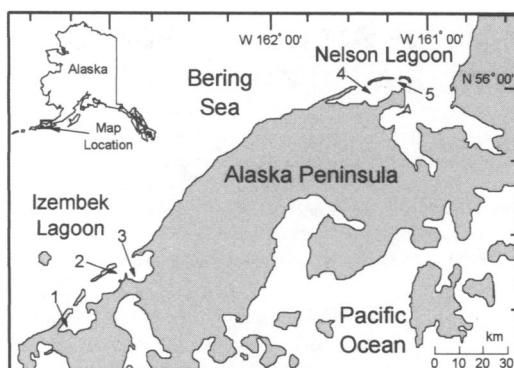[1] E-mail: ghepp@acesag.auburn.edu

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Fig. 1. Map of areas where Steller's eiders were captured along the Alaska Peninsula. Numbered areas refer to specific locations used as 'states' in multi-state analyses.

(*Branta bernicla nigricans*) had high rates of fidelity (95%) to specific molting locations. Recaptures of previously banded birds provide evidence that some level of molting site fidelity exists for a few species of ducks (Anderson and Sterling 1974, Williams 1979, Szymczak and Rexstad 1991, Bowman and Brown 1992). Szymczak and Rexstad (1991) report that >67% of recaptures of molting gadwall (*Anas strepera*) occurred in the same wetland as the original banding. Whereas, Bowman and Brown (1992) found that 52% of black ducks (*Anas rubripes*) were recaptured on the same wetland as the original banding. Therefore, there is limited evidence for fidelity to specific molting areas for some species of ducks; however, detailed estimates of fidelity rates and movement probabilities are lacking.

It was the goal of this project to determine annual survival rates for male and female Steller's eiders molting along the Alaska Peninsula. We compare survival estimates based on data from the 1990's to estimates based on data collected in the late 1970's. Further, we examine fidelity to molting areas and patterns of movement within and among lagoons.

METHODS

Steller's eiders were captured during wing molt at Izembek (55°20′N, 162°50′W) and Nelson (56°00′N, 161°20′W) lagoons, Alaska, from late August through early October (Fig. 1). Flightless birds were herded with boats along tide channels and driven out of the water into corral traps of nylon net placed on beaches. Each bird was marked with a U.S. Fish and Wildlife Service metal band. The band number

of previously marked birds was recorded or the band was replaced if the number was illegible due to wear. Prior to 1993 most bands used were aluminum, however, 600 monel bands and 194 incoloy bands were used from 1975–78 and in 1980, respectively. Additionally, stainless steel, aluminum, and incoloy bands were used from 1993–97. Aluminum bands removed due to band wear were weighed to the nearest 0.0001 g and etched using a solution of hydrochloric acid and cupric ammonium chloride to facilitate reading the number.

Analysis

We used regression analysis to examine band weight in relation to band age for aluminum bands removed for replacement. We assumed normal variation in band weight within band ages. We recovered the lightest band (0.4 g) on the ground following a banding drive. Therefore, we assumed that bands degraded to this weight would be lost. We modeled band loss using the rate of decay predicted from regression, normal variation in band weight within cohorts (i.e., band age), and a minimum band weight below which all bands were assumed lost. From these data, we estimated the proportion of aluminum bands of each age class that were below the minimum band weight. This can be thought of as a series of normal distributions, each centered on the regression line. We then estimated the proportion of each distribution that occurred below the 0.4-g minimum. Previous studies of band loss also have used changes in band weight through time and changes in variation in band weight within cohorts to estimate loss (Ludwig 1967, Hatch and Nisbet 1983).

Because molting Steller's eiders concentrate in channels at low tide, we subdivided each lagoon into specific locations based on geography of tide channels, lagoon entrances, and distribution of birds (Fig. 1). Given the distance between areas, birds molting in different areas are functionally isolated during the flightless period. Female ducks typically have lower survival than males (Johnson et al. 1992); therefore, we modeled survival of males and females separately; and, we did not consider models in which male and female survival were equal. In fact, for one analysis we separated the data sets for males and females to reduce the parameter space. Our banding efforts varied annually and our success in capturing eiders varied due to factors

Table 1. Number of Steller's eiders captured by location and year along the Alaska Peninsula. See Fig. 1 for specific locations within lagoons.

| | Banding location[a] | | | | |
| | Izembek Lagoon | | | Nelson Lagoon | |
Year	1	2	3	4	5
1975	890[b]				
1976	497[b]				
1977	1,442[b]				
1978	557[b]				
1979	517[b]				
1980	987[b]				
1981	1,063[b]				
1991	56[b]				
1992	584[b]				
1993	3,512[b,c]	2,873[c]			
1994	2,307[b,c]	2,989[c]			
1995	2,269[b,c,d]	5,828[c,d]	256[d]	5,906[d]	4,514[d]
1996	1,207[b,c,d]	3,512[c,d]	820[d]	4,567[d]	4,272[d]
1997	704[b,c,d]	3,628[c,d]	11[d]	1,484[d]	6,149[d]
Totals	16,593	18,832	1,090	11,961	14,940

[a] Blanks indicate no capture effort.
[b] Indicates data used for historical comparisons.
[c] Indicates data used for estimates of survival and non-Markovian movement probabilities within Izembek lagoon.
[d] Indicates data used to examine geographic variation in survival rate and movement probabilities among lagoons.

such as weather, experience of personnel, and mechanical failure of boats (Table 1). Accordingly, we expected variation in recapture rate and we only considered models where recapture rates were allowed to vary by year, sex, and location. One additional capture event at area 2 in 1984 (Fig. 1) was excluded from analyses as these data were not useful in the analyses we conducted (Table 1).

We conducted 3 sets of survival analyses. For each, we calculated $\hat{c}$ (i.e., variance inflation factor) from the goodness-of-fit statistics from the most general model as an indicator of overall structural fit (Burnham and Anderson 1998). Values of $\hat{c} < 3$ were assumed to indicate overdispersion of the data (Anderson et al. 1994) as opposed to inappropriate model structure (Burnham and Anderson 1998). We used $\hat{c}$ to adjust the Akaike's information criterion (AIC) and standard errors of parameter estimates; an AIC value adjusted for variance inflation is referred to as a quasi-likelihood AIC (i.e., QAIC). In all analyses we used AIC or QAIC as the model selection criteria (Anderson et al. 1994). Model notation follows that of Lebreton et al. (1992) where subscripts are used to denote variation in a given model component. Model components are defined as: ϕ = probability of survival, ψ = probability of movement, ρ = probability of recapture. Subscripts are defined as: l = recapture location, t = time, s = sex, m designates non-Markovian movement probabilities (i.e., memory model, see below). Use of one of these lettered subscripts implies model components varied by that subscript. Use of a dot in the subscript implies that model component was constant. For example, the notation $\phi_{s\bullet\bullet}\psi_{sl\bullet}\rho_{slt}$ denotes survival as varying among sexes but was constant among locations and years, movement probabilities varied among sexes and locations but was constant among years, and recapture probability varied among sexes, locations, and years.

We had 3 main goals in our survival analyses. First, we sought to estimate a current survival rate for male and female Steller's eiders. To accomplish this, we used data from 1993–97 at Izembek Lagoon (Table 1). We started with general models treating locations within the lagoon as 'states' in a multi–state approach using program MSSURVIV (Brownie et al. 1993). These models included a term that considered the location where an individual was captured and estimated the probability that a bird present in location a at time i is present in location b at time $i + 1$, given that it survived the interval. Thus, the use of multi–state models allows simultaneous inference regarding survival and site fidelity. We also examined non-Markovian transition models that take into account the previous location of birds (i.e., at time $i - 1$; Hestbeck et al. 1991, Brownie et al. 1993). Once a general model that adequately fit these data was found, we explored reduced parameter models that made biological sense.

Second, we sought to examine evidence that annual survival rates varied among different molting populations. To accomplish this we used data from 1995–97 from Izembek and Nelson lagoons (Table 1). We used a multi–state approach comparing 3 locations within Izembek Lagoon and 2 locations within Nelson Lagoon. Because we only had 3 years of data for both lagoons we could not employ non-Markovian models (Table 1). Given a general model, we then examined reduced parameter models using the same criteria as above.

Finally, we sought to determine if there had been a reduction in survival over time. To accomplish this we used data from 1975–81 and 1991–97 at Izembek Lagoon. Because we only had historic data from 1 location (Table 1), we used a standard Cormack-Jolly-Seber approach
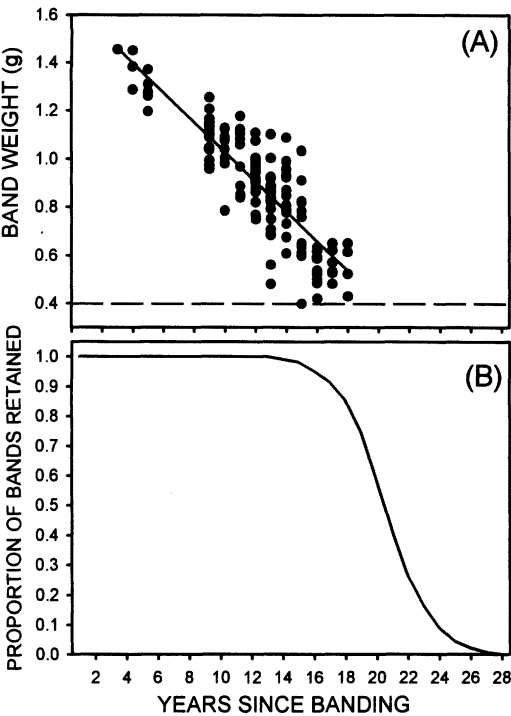
Fig. 2. (A) Relationship between age of band and band weight for aluminum bands recovered from Steller's eiders molting along the Alaska Peninsula. (B) Estimated loss function for aluminum bands placed on Steller's eiders using the rate of decay (from A) and a threshold for minimum band weight resulting in loss (dashed line).

Table 2. AIC comparisons among models used to estimate adult survival and movement probabilities of Steller's eiders molting at Izembek Lagoon, Alaska 1993–97.

Model[b]	Δ AIC[a]	
	Females	Males
$\phi_{\bullet\bullet} \psi_{l\bullet m} \rho_{lt}$	0.00	0.00
$\phi_{l\bullet} \psi_{l\bullet m} \rho_{lt}$	1.56	0.88
$\phi_{l^*\bullet} \psi_{l\bullet m} \rho_{lt}$	5.24	4.53
$\phi_{lt} \psi_{l\bullet m} \rho_{lt}$	18.82	6.29
$\phi_{lt} \psi_{lt} \rho_{lt}$	63.27	16.30

[a] Increase in Akaike's information criterion (AIC; Anderson et al. 1994) over the lowest observed value of AIC.
[b] Notation follows that of Lebreton et al. (1992). ϕ = probability of survival, ψ = probability of movement, ρ = probability of recapture, l = recapture location, t = time, m designates non-Markovian movement probabilities (i.e., memory model). l* denotes survival as varying among locations and birds that moved vs. those that remained at the previous location.

survival for a given sex and period

$$= \frac{e^{sex+period}}{1 + e^{sex+period}}.$$

RESULTS

We captured a total of 63,401 Steller's eiders across all years (Table 1). The sex ratio of captured Steller's eiders differed among banding areas. The proportion of females captured ($\pm$SE) in areas 1–5 (Fig. 1) was: 0.791 $\pm$ 0.003, 0.404 $\pm$ 0.004, 0.977 $\pm$ 0.005, 0.384 $\pm$ 0.004, and 0.215 $\pm$ 0.003.

The band loss function suggests that retention is high until about 15 years after banding (Fig. 2). This function predicts that by 20 years postbanding, 50% of aluminum bands will have been lost. Based on these results, we assumed no band loss for birds recaptured less than 10 years after banding.

Current Survival and Movement

We modeled survival and movement probabilities of each sex separately. A non-Markovian model based on capture location (commonly referred to as a memory model) fit these data for both sexes ($\hat{c}$ = 1.09 for females and $\hat{c}$ = 1.00 for males) better than a standard multi–state model ($\hat{c}$ = 12.2). For both sexes, the most parsimonious model was when survival did not vary over time or location and movement probabilities did not vary over time (Table 2). Estimates of annual survival were 0.899 $\pm$ 0.032 for females and 0.765 $\pm$ 0.044 for males. Most birds were recaptured in the same location in subsequent years (Table 3). Of the females that changed locations, about half were recaptured

(Pollock et al. 1990) and program MARK. We considered these 2 time periods as separate data sets because we assumed there was some band loss for periods >12 years postbanding. Thus, birds captured after 1991 that were originally banded between 1975 and 1981 were considered newly marked birds and any additional recapture information (i.e., after 1991) was not used in survival estimation for the early period. We used variance inflation factors (i.e., $\hat{c}$) calculated from the goodness-of-fit tests in program RELEASE (Burnham et al. 1987) to adjust the AIC and standard errors of parameter estimates, as suggested by Lebreton et al. (1992). We considered time periods as groups, but allowed recapture probability to vary by year and sex within periods. We considered models in which survival differed by sex and period (4 parameters), sex (2 parameters), and an additive model with the same adjustment to survival across periods was applied to each sex using a logit–linked model (3 parameters, one for each sex and one for the effect of periods). Therefore,

Table 3. Estimates of non-Markovian movement probabilities ($\hat{\psi}$) for Steller's eiders molting at 2 locations within Izembek Lagoon, Alaska 1993–97.

Recapture history[a]	Females		Males	
	$\hat{\psi}$	SE	$\hat{\psi}$	SE
111	0.955	0.010	0.780	0.058
112	0.045	0.010	0.220	0.058
121	0.513	0.115	0.306	0.147
122	0.487	0.115	0.694	0.147
211	0.524	0.120	0.369	0.282
212	0.476	0.120	0.631	0.282
221	0.032	0.016	0.030	0.003
222	0.968	0.016	0.970	0.003

[a] Numbers refer to capture locations identified on Fig. 1 at $t = i - 1$, $t = i$, and $t = i + 1$. Movement probabilities ($\hat{\psi}$) are the probability that a bird present in a location at $t = i$ is present in location b at $t = i + 1$. For example, of females captured at location 1 in year $i - 1$ and recaptured in location 2 in year i, 51.3% moved back to location 1 in year $i + 1$ (recapture history 121) and 48.7% remained at location 2 in year $i + 1$ (recapture history 122).

again at their new location and the remainder returned to the original banding location. For males there appears to be directional movement from area 1 to area 2 (Table 3).

Geographic Variation in Survival

Our data were not sufficient to solve for parameter estimates using multi–state models allowing survival, movement, and recapture probabilities to vary among years. Therefore, we used the goodness-of-fit results from a multi–state model where survival and movement probabilities were constant and recapture probability varied among years (model B from Pollock et al. 1990) to estimate the variance inflation factor ($\hat{c} = 1.918$). In the most parsimonious model, survival varied among sexes but not among capture locations ($\phi_{s\bullet\bullet}\psi_{sl\bullet}\rho_{slt}$). In the alternative models, survival varied among lagoons (noted as l*) ($\phi_{sl}*_\bullet\psi_{sl\bullet}\rho_{slt}$; ΔQAIC = 2.48) or among all capture locations ($\phi_{sl\bullet}\psi_{sl\bullet}\rho_{slt}$; ΔQAIC = 9.39). Both sexes showed high fidelity to specific lagoons (Table 4).

Temporal Variation in Survival

We used a Cormack–Jolly–Seber model and the results from the goodness–of–fit tests in program RELEASE to estimate the variance inflation factor ($\hat{c} = 2.463$). We found no evidence of variation in survival within time periods; however, we found some evidence for variation in survival among time periods. In the most parsimonious model for these data, survival for both sexes declined between time periods based on a logit model (noted as t*) ($\phi_{st}*\rho_{st}$). In the

Table 4. Estimated movement probabilities ($\hat{\psi}$) among lagoons for Steller's eiders molting along the Alaska Peninsula.

Recapture history	Females		Males	
	$\hat{\psi}$	SE	$\hat{\psi}$	SE
Philopatry to Izembek	0.984	0.015	0.951	0.038
Izembek to Nelson	0.016	0.015	0.049	0.038
Nelson to Izembek	0.014	0.018	0.004	0.003
Philopatry to Nelson	0.986	0.018	0.996	0.003

best alternative models, survival varied among time periods and sexes ($\phi_{st}\rho_{st}$, ΔQAIC = 1.53) or survival was constant across time periods ($\phi_{s\bullet}\rho_{st}$, ΔQAIC = 1.58). Thus, based on QAIC, we conclude that survival of both males and females declined since the 1975–81 period. The estimate of annual survival for adult females from 1975 to 1981 was 0.946 ± 0.059 compared to 0.827 ± 0.018 from 1991 to 1997. Similarly, the estimate of annual survival for adult males from 1975 to 1981 was 0.874 ± 0.062 compared to 0.761 ± 0.050 from 1991 to 1997.

DISCUSSION

Our estimates of annual rates of survival for adult female Steller's eiders are similar to common eiders (*Somateria mollissima*; Reed 1975, Wakeley and Mendall 1976, Coulson 1984), but higher than spectacled eiders (*Somateria fischeri*; Grand et al. 1998). We found no evidence that annual survival rate of Steller's eiders varied among years within specific time periods (i.e., 1993–97). However, we found some evidence that survival rates may have declined between time periods (i.e., late 1970's to early 1990's), although the difference in QAIC values between models was small (i.e., ΔQAIC = 1.53). Burnham and Anderson (1998) state that models having similar QAIC values to the best model (i.e., differing by ≤2) deserve consideration in making inferences. While we conclude that the best model for our data is one in which survival has declined through time, evidence for this decline is weak. Population models for other waterfowl suggest that a reduction in annual survival of the magnitude we estimated (i.e., ≈9%) would have a substantial negative effect on population dynamics (Schmutz et al. 1997, Flint et al. 1998). Therefore, a reduction in adult survival may be an underlying cause of the population decline of Steller's eiders. Potential causes of this apparent change in adult survival are unknown.

Female Steller's eiders had higher survival

than males, which is unusual for waterfowl. Typically, survival of females is lower than males (Johnson et al. 1992). Lower survival for female waterfowl has been hypothesized to be the result of increased risk associated with breeding (specifically, incubation and brood rearing; Sargeant et al. 1984, Cowardin et al. 1985, Sargeant and Raveling 1992). It is not clear why patterns of survival among Steller's eiders might differ from those of other ducks. Male Steller's eiders, like males of other duck species, abandon females after egg laying is complete and depart the breeding grounds. We do not know where male Steller's eiders go between the time they abandon their mates (early June) and their arrival on molting areas (late July). High mortality during this period may be responsible for the lower survival of males as the sexes are likely sympatric throughout the remainder of the year. Assuming an equal sex ratio at hatch, the difference in survival between sexes we report would result in a female-biased sex ratio (Johnson and Sargeant 1977). Thus, a shortage of drakes may prevent all females from pairing and reduced breeding propensity may be limiting the reproductive potential of Steller's eiders.

We found little evidence that annual survival rate varied for either males or females among different molting locations. Within Izembek Lagoon, the non-Markovian transition model where survival differed between areas 1 and 2 had a similar AIC value to a model with constant survival across areas (Table 2). However, the model with geographic variation in survival rate was not supported in the larger data set incorporating birds banded at locations in both Izembek and Nelson Lagoons. Therefore, we conclude that survival did not vary among molting locations for either sex. If birds molting in a specific location also breed in a specific geographic location, it is possible that risk factors differ among these subpopulations resulting in variation in survival among molting populations. Individual Steller's eiders had high fidelity to specific molting locations, yet we do not know the associated breeding distributions. Therefore, it is not clear whether individual molting concentrations can be considered unique subpopulations. For example, black brant show high levels of fidelity to both breeding (Lindberg and Sedinger 1997, Lindberg et al. 1998) and molting locations (Bollinger and Derksen 1996). Bollinger and Derksen (1996) found that black brant molting on specific lakes were from

multiple breeding colonies. Under this scenario, molting populations of Steller's eiders would not be unique subpopulations and it would be unlikely that survival would differ among birds using different molting areas. Our data suggest that either molting locations do not represent unique subpopulations or survival probability does not vary among subpopulations. Additional data on linkages between molting and breeding locations are required to distinguish between these explanations.

Our data demonstrate that Steller's eiders exhibit very high fidelity to specific molting areas. The rates of fidelity for Steller's eiders exceed estimates of fidelity rates for other ducks (Anderson and Sterling 1974, Williams 1979, Szymczak and Rexstad 1991, Bowman and Brown 1992) and are similar to those reported for geese (e.g., black brant; Bollinger and Derksen 1996). In all analyses, Steller's eiders were most likely to be recaptured in the location (within lagoons) where they were captured previously. When birds moved among specific molting areas within Izembek Lagoon (i.e., areas 1 and 2), the non-Markovian transition probabilities suggest that about half return to the original banding location. Anderson et al. (1992) discussed the potential advantages of fidelity to breeding locations; however, most of these hypotheses cannot explain fidelity to molting areas. Environmental variability is likely linked to fidelity such that birds using temporally consistent habitats are more likely to have high fidelity (Spaans 1977). Certainly, the overall habitat conditions in these Bering Sea lagoon systems are relatively consistent across years and are not influenced by annual weather fluctuations to the same extent as freshwater wetlands. For individual Steller's eiders, the advantages of returning to a specific molting location within a lagoon are unknown. Hohman et al. (1992) suggest that advantages might include familiarity with available resources and shelter. Steller's eiders molt in large flocks and the sexes tend to segregate among molting locations. Without an understanding of the factors influencing this molting distribution, it is difficult to speculate on the potential advantages of site fidelity for molting. The molting ecology of Steller's eiders along the Alaska Peninsula deserves further study.

MANAGEMENT IMPLICATIONS

Given that survival appears to have declined over the last 20 years, managers should examine

mortality factors that may have caused this trend. Specifically, managers should focus on determining factors that influence adult male survival. Determination of sex ratios in the overall population is essential for assessment of reproductive potential. The high rates of fidelity to molting areas imply that management activities or disturbances at molting areas may adversely affect specific subpopulations of birds and protection of these molting areas maybe important. Understanding the linkage between breeding and molting distributions is required for interpreting the impact of management actions or disturbances on subpopulations of molting Steller's eiders.

ACKNOWLEDGMENTS

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